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Anthropogenic resource subsidies decouple predator–prey relationships

Amanda D. Rodewald,[1,3] Laura J. Kearns,[1] and Daniel P. Shustack[2]

[1]*School of Environment and Natural Resources, Ohio State University, Columbus, Ohio 43210 USA*
[2]*Biology Department, Massachusetts College of Liberal Arts, 375 Church Street, North Adams, Massachusetts 01247 USA*

Abstract. The extent to which resource subsidies affect food web dynamics is poorly understood in anthropogenic landscapes. To better understand how species interactions are influenced by subsidies, we studied breeding birds and nest predators along a rural-to-urban landscape gradient that varied in subsidies provided to generalist predators. We hypothesized that resource subsidies in urban landscapes would decouple predator–prey relationships, as predators switch from natural to anthropogenic foods. From 2004 to 2009, we surveyed nest predators and monitored 2942 nests of five songbird species breeding in 19 mature forest stands in Ohio, USA. Eighteen species were video-recorded depredating nests. Numbers of avian and mammalian nest predators were positively associated with the amount of urban development surrounding forests, with the exception of Brown-headed Cowbirds (*Molothrus ater*). Although nest survival strongly declined with detections of nest predators in rural landscapes, nest survival and predator numbers were unrelated in urban landscapes. Thus, the strength of interaction between breeding birds and nest predators diminished as landscapes surrounding forested parks became more urbanized. Our work suggests that decoupling of predator–prey relationships can arise when synanthropic predators are heavily subsidized by anthropogenic resources. In this way, human drivers can alter, and completely disarticulate, relationships among species that are well established in more natural systems.

Key words: birds; forest; landscape; nest predation; nest survival; predator; prey; resource subsidy; species interactions; urban–rural gradient.

Introduction

Assembly and organization of animal communities over evolutionary and contemporary time scales are shaped by species interactions, which have long been a focal point of community ecology (Elton 1927). Interactions between predator and prey species, in particular, can play important roles in regulating populations and structuring communities (Hairston et al. 1960, Fretwell 1987). Indeed, predator–prey interactions have profoundly influenced the evolution of life history traits and breeding ecology of birds, as nest predation is the major source of avian reproductive failure in most systems (Ricklefs 1969, Martin 1988). The impact of predators on reproductive success generally increases with abundance and/or activity of nest predators (e.g., Andrén 1992; Zanette and Jenkins 2000, Weidinger 2002), though loss of apex predators also can reduce nest survival via mesopredator release (Rogers and Caro 1998, Crooks and Soulé 1999, Terborgh et al. 2001, Rayner et al. 2007).

Though most frequently studied in rural or wild landscapes, interactions between breeding birds and their predators are considered to be one of the potential drivers of urban-associated shifts in avian community structure (Faeth et al. 2005, Shochat et al. 2006). Urban systems typically support high densities of a variety of generalist and opportunistic predators (Crooks and Soulé 1999, Sorace 2002, Prange and Gehrt 2004, Chace and Walsh 2006) and relatively sparse numbers of insectivorous and sensitive avian species (Beissinger and Osborne 1982, Rodewald and Bakermans 2006). The concomitant increase in nest predators and decrease in sensitive avian species is suggestive that nest predation shapes patterns in community structure. Yet assuming that numerical increases in predators result in greater nest predation pressure overlooks the potential influence of human activity on species interactions. Human activities can change the nature of predator–prey relationships both by directly manipulating numbers of predators and prey and by providing resource subsidies. Subsidies, which are resources provided by a donor (in this case, humans) to a recipient, can dramatically increase productivity of the recipient population and affect food web dynamics (Polis et al. 1997, Marczak et al. 2007). The extent to which resource subsidies alter species interactions in anthropogenic landscapes has received little attention.

Urban systems present an excellent opportunity to understand how spatial subsidies affect predator–prey relationships. A defining characteristic of many urban habitats is the rich assortment of anthropogenic

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[3] E-mail: rodewald.1@osu.edu

TABLE 1. Daily survival rates of nests for five forest-breeding songbirds in Ohio, 2004–2009.

Species	Daily nest survival					
	2004	2005	2006	2007	2008	2009
Acadian Flycatcher	0.981 (72)	0.979 (78)	0.975 (75)	0.974 (72)	0.971 (75)	0.945 (65)
American Robin	0.946 (67)	0.969 (74)	0.912 (46)	0.946 (52)	0.945 (73)	0.939 (105)
Gray Catbird	0.953 (27)	0.944 (7)	0.940 (4)	0.976 (29)	0.960 (36)	0.948 (57)
Northern Cardinal	0.945 (195)	0.949 (306)	0.937 (289)	0.952 (378)	0.947 (269)	0.902 (366)
Wood Thrush	0.958 (22)	0.964 (21)	0.955 (12)	0.977 (22)	0.972 (27)	0.967 (21)

Note: Numbers of nests monitored annually are indicated in parentheses.

resources, whether in the form of bird feeders, food placed to attract mammalian species, or human refuse in predictable and unpredictable locations. Resource subsidies can lead to cross-edge spillover of subsidized predators from urban to natural areas (Rand et al. 2006) as well as functional and/or numerical responses of predators (Ostfeld and Keesing 2000, Faeth et al. 2005), any of which might have demographic or behavioral consequences in prey populations. For example, anthropogenic foods present in remote campgrounds and human settlements attracted and promoted survival and reproduction of American crows (*Corvus brachyrhynchos*) and other corvids in Washington (Marzluff and Neatherlin 2006). Similarly, corvid activity is oftentimes concentrated near predictable food sources (Martin and Joron 2003).

To better understand how species interactions are influenced by resource subsidies, we studied breeding birds and nest predators in forests along a rural-to-urban landscape gradient. We hypothesized that subsidies provided in urban landscapes would decouple predator–prey relationships, as generalist predators presumably switched from natural to anthropogenic food sources. Specifically, we predicted that the relationship between nest survival and numbers of nest predators would diminish as the landscapes surrounding forested parks urbanized.

METHODS

From 2004 to 2009, we monitored 2942 nests of five forest-breeding songbird species in 19 mature riparian forest stands distributed along a rural-to-urban landscape gradient in central Ohio, USA (approximately 39°50′ N–40°21′ N; 82°50′ W–83°14′ W). Landscapes across our rural-to-urban gradient shared similar land use history as well as amount and spatial configurations of natural areas. Forests varied in width (115–565 m for >300 m of length), but the width of the forest was not confounded with the amount of surrounding urban development ($r = -0.015$, $P = 0.546$). Thus, sites located along the rural–urban gradient differed primarily in the dominant land use type within the landscape matrix. As part of a complementary study, we calculated an urban index based for each site on measures of landscape composition within 1 km based on digital orthophotos from 2002–2004 (see Rodewald and Shustack 2008). The urban index was strongly correlated with number of buildings (0.92), percent cover by roads (0.94), pavement (0.90), and lawn (0.88), but negatively with percent cover by agriculture/pasture (–0.83). Building densities in our landscapes ranged from 0.1–7.3 buildings per ha (10–727 buildings/km^2).

From March to September, we searched forest habitats for nests of five songbird species that bred in understory and midstory strata: one resident (Northern Cardinal, *Cardinalis cardinalis*, $n = 1803$), one temperate migrant (American Robin, *Turdus migratorius*, $n = 417$), and three Neotropical migratory species (Acadian Flycatcher, *Empidonax virescens*, $n = 437$; Gray Catbird, *Dumetella carolinensis*, $n = 160$; Wood Thrush, *Hylocichla mustelina*, $n = 125$; Table 1). Our previous work in this system indicated that Robins and Cardinals (and Catbirds, to a lesser extent) respond positively to urbanizing landscapes, whereas the Acadian Flycatcher and Wood Thrush respond negatively (Rodewald and Bakermans 2006). Regionally, Acadian Flycatcher and Wood Thrush are considered to be species of conservation importance. Each located nest was checked at 2–4-day intervals by viewing nest contents or by observing parental behavior to track nest stage (e.g., onset of incubation behavior) and locate young fledglings, when possible. To avoid exposing nests to predators as a consequence of our visits, we checked actual nest contents infrequently, and observed nests from as far a distance as possible (often >10 m), for as brief a time as possible, and from different routes each time (Göttmark 1992). If a predator was observed in the vicinity, we delayed checking the nest.

From 2007 to 2009, we used time-lapse video systems to identify species responsible for nest depredation events. Video systems consisted of miniature cameras, time-lapse digital recorders in weatherproof cases, and infrared light-emitting diodes to allow filming in darkness (950 nm; not visible to vertebrates). Several systems were custom built by Fuhrman Diversified, Inc. (FIELDCAM Miniature Digital SD4TLV; Seabrook, Texas, USA) and several were built by us using a design developed by F. R. Thompson III and W. A. Cox. As recommended by Richardson et al. (2009), our cameras were small, highly camouflaged, placed so as to avoid manipulating nest concealment, widely dispersed (i.e., camera-monitored nests were not clumped within a

predator's home range), and deployed in small numbers (usually—one or two cameras) at a site at any given time. Across the rural-to-urban gradient, nests with cameras had similar visitation/check rates, and this reduces the possibility of bias. Although a recent meta-analysis suggests that camera-monitored nests may be relatively less likely to be depredated than unmonitored nests (Richardson et al. 2009), we used nest cameras, not to estimate risk of predation, but to identify the suite of nest predators (Thompson and Burhans 2003, Reidy et al. 2008). We do not expect that our estimates of overall predation are affected by our use of cameras given that the number of nests with cameras was small relative to the total number of nests that we monitored (<3%).

Based on our video-recordings of 67 depredation events, we identified 18 different species of nest predators. Avian predators included American Crow, Blue Jay (*Cyanocitta cristata*), Barred Owl (*Strix varia*), Cooper's Hawk (*Accipiter cooperii*), Red-tailed Hawk (*Buteo jamaicensis*), Red-shouldered Hawk (*Buteo lineatus*), Broad-winged Hawk (*Buteo platypterus*), Common Grackle (*Quiscalus quiscala*), and Brown-headed Cowbird (*Molothrus ater*). We also recorded two cases of Gray Catbird and one case of Northern Cardinal removing eggs from nests. Mammalian predators of nests were raccoon (*Procyon lotor*), domestic cat (*Felis catus*), Eastern gray squirrel (*Sciurus carolinensis*), red squirrel (*Tamiasciurus hudsonicus*), and Virginia opossum (*Didelphis virginiana*). We had one record each for black rat snake (*Elaphe obsoleta*) and Eastern garter snake (*Thamnophis sirtalis*). At the species level, cowbirds and raccoons were co-dominant predators, but each represented only 15% and 13% of depredations, respectively. All other predator species accounted for <7% of recorded depredations.

At weekly intervals between May and July 2004–2009, we surveyed nest predators 10 times at each site within 2-ha grids flagged at 50-m intervals. During surveys a trained observer systematically traversed the entire marked grid over an approximately 45-minute period between 05:45 and 10:00 and recorded all nest predators seen or heard. Although we also conducted timed substrate searches for snakes, we detected few individuals and could not consider snakes in our analysis. We created an annual mean index of predator abundance for each species by dividing the total number of predator detections by the number of visits to a site per year. Because this index is based upon number of detections, it better represents the relative activity than actual densities or numbers predators among sites. Responses of predators to urbanization within the landscape matrix were examined separately for raptors (i.e., all hawks and owls), corvids (i.e., Blue Jay, American Crow), Common Grackles, Brown-headed Cowbirds, squirrels (i.e., Eastern gray and red squirrels), native mesopredators (i.e., opossum and raccoon), and cats. For groups containing multiple species, we added their mean predator abundances to create a single index. Separately for each group, we used the annual index of predator abundance or activity in a repeated measures regression (with a negative binomial distribution) to test for a relationship between predators and urbanization.

Daily nest survival rates (DSR) were estimated for each site in each year using the logistic exposure model. The logistic exposure model is a generalized linear model that specifies a binomial error distribution and a link function similar to a logit link function adjusted for length of exposure for each nest using SAS 9.1 (SAS Institute 2002, Shaffer 2004). The logistic exposure model estimates probability of nest survival between each visit to the nest, thereby eliminating potential bias due to different exposure periods. Nest fate at each nest check was modeled as either failing (0) or surviving (1) the nest-check interval. We omitted nests whose failure was confirmed to be unrelated to predators (e.g., weather; <0.25% of failed nests). Based on observations of nest contents and/or parental behavior, we estimate that predation was responsible for >90% of nest failures. For some nests that failed early in the nesting cycle prior to our confirmation that a clutch had been laid, we were unable to determine with absolute certainty that nests had been depredated rather than abandoned. However, the high rates of depredation at our sites, especially early in the breeding season, make it likely that we failed to detect predation in some cases.

Given the high diversity and evenness of the nest predator community (i.e., individual species accounted for only 1–15% of all depredations), we summed the annual mean indices of predator abundances for each species into a single index of predator abundance. This index was significantly correlated with detections of raptors (Spearman rho = 0.162, $P = 0.004$), corvids (Spearman rho = 0.291, $P < 0.001$), Common Grackles (Spearman rho = 0.457, $P < 0.001$), Brown-headed Cowbirds (Spearman rho = 0.651, $P < 0.001$), native mesopredators (Spearman rho = 0.291, $P < 0.001$), squirrels (Spearman rho = 0.708, $P < 0.001$), and cats (Spearman rho = 0.378, $P < 0.001$), as well as combined avian (Spearman rho = 0.793, $P < 0.001$) and mammalian (Spearman rho = 0.719, $P < 0.001$) predators.

We used repeated-measures regression (proc Mixed; SAS, 9.1) to examine the extent to which relationships between predators and prey were influenced by urbanization. We combined nests across species because our preliminary analyses conducted separately for each species showed similar patterns of response. In our models, we avoided pseudoreplication by using DSR for each site in a given year as the response variable and explicitly included year in a repeated measures design. We tested the main effects of urbanization and number of nest predators as well as the interaction between urbanization and numbers of predators. Multicollinearity was thought not to be a serious issue because (1) the correlation coefficient between predator

numbers and the urban index was 0.44 which is far below the 0.7 level that typically indicate problems and (2) variance inflation factors for all terms were <10, which is a common and relatively conservative rule of thumb (O'Brien 2007).

Results

The amount of urban development surrounding riparian forests was positively associated with numbers of squirrels ($\beta = 0.86 \pm 0.10$ [mean $\pm$ SE]; $\chi^2 = 5.39$, $P = 0.020$; mean detections per visit = 1.3 ± 0.03), raptors ($\beta = 0.64 \pm 0.166$; $\chi^2 = 4.25$, $P = 0.039$; mean detections per visit = 0.01 ± 0.0004), free-ranging domestic cats ($\beta = 0.92 \pm 0.158$; $\chi^2 = 4.0$, $P = 0.045$; mean detections per visit = 0.02 ± 0.002), Common Grackles ($\beta = 0.28 \pm 0.068$; $\chi^2 = 4.03$, $P = 0.045$; mean detections per visit = 0.26 ± 0.005), corvids ($\beta = 0.12 \pm 0.053$; $\chi^2 = 3.67$, $P = 0.056$; mean detections per visit = 0.31 ± 0.005), and native mesopredators ($\beta = 0.75 \pm 0.197$; $\chi^2 = 3.62$, $P = 0.057$; mean detections per visit = 0.014 ± 0.0006). Brown-headed Cowbird was the only species of nest predator not significantly associated with urbanization ($\beta = -0.02 \pm 0.043$; $\chi^2 = 0.18$, $P = 0.668$; mean detections per visit = 0.78 ± 0.01).

Over 6 years, daily nest survival averaged 0.953 ± 0.002, with annual survival estimates ranging from 0.92 ± 0.008 to 0.97 ± 0.004, which translates to 16–48% apparent nesting success (22-day nesting cycle). DSR generally declined with increasing numbers of predators ($\beta = -0.006 \pm 0.002$; $F_{1,78} = 10.85$, $P = 0.002$) and urbanization surrounding a site ($\beta = -0.011 \pm 0.004$; $F_{1,78} = 8.51$, $P = 0.005$). However, we found that the relationship between abundance of nest predators and DSR depended upon the amount of urbanization within the matrix surrounding the forest ($\beta = 0.004 \pm 0.002$; $F_{1,78} = 8.63$, $P = 0.004$; Fig. 1). The statistically significant interaction makes tests of main effects unreliable. Nest survival strongly declined with increasing predator detections only in the rural landscapes. In urban landscapes, there was no relationship between DSR and predator activity. This same pattern also was evident when avian species were examined individually (Fig. 2).

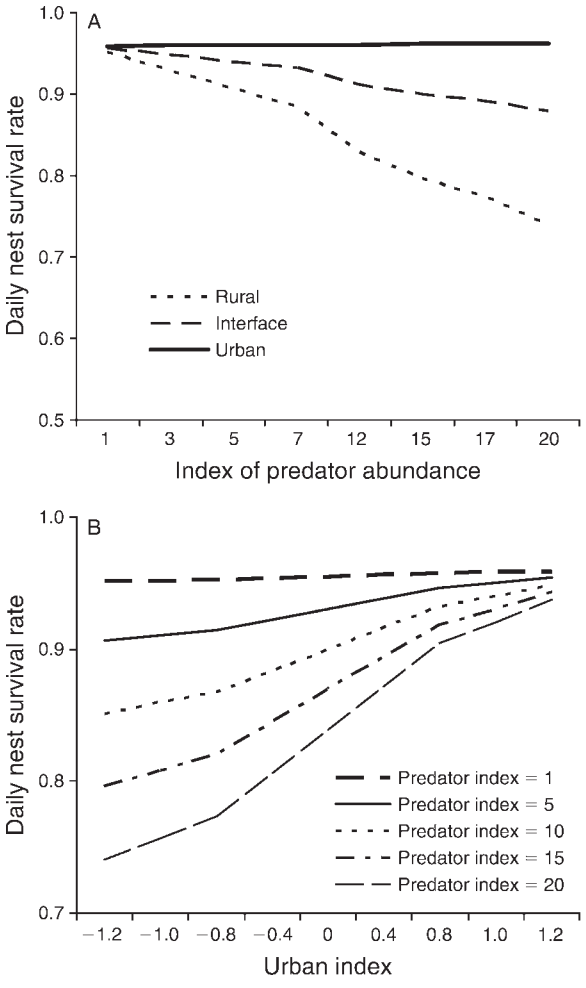

FIG. 1. Relationship between daily survival of 2942 nests and an index of predator abundance is landscape dependent, such that nest survival does not decline with predator numbers in urban landscapes. For illustrative purposes only, we graphed relationships for (A) three values of the urban index to represent urban (urban index = 1.5), urban–rural interface (urban index = 0), and rural (urban index = −1.2) landscapes and (B) five levels of the index of predator abundance. Relationships were modeled using the following equation derived from our repeated-measures regression for daily nest survival rates (DSR): DSR = 0.961 − 0.0061(number of predators) − 0.0114 (urban index) + 0.0042(predators × urban).

Discussion

Our six-year study suggests that an urbanizing landscape matrix can decouple interactions between breeding birds and their nest predators, such that the two are no longer interrelated. Avian nest survival strongly declined with detections of known species of nest predators in the rural landscapes. In urban landscapes, however, the relationship between DSR and predator activity was almost entirely decoupled. For example, an increase in predator numbers from 1 to 20 reduced DSR by 22% (from 0.95 to 0.74) in rural landscapes, but slightly increased DSR in urban landscapes. We suggest that the lack of concordance between rates of nest predation and predator activity in urban landscapes arises because many synanthropic predators are heavily subsidized by anthropogenic food sources (Gehrt 2004, Prange et al. 2004, Marzluff and Neatherlin 2006, Withey and Marzluff 2009) and, consequently, may depredate fewer nests than less subsidized rural predators. Both theoretical (Schmidt 1999) and empirical studies (Miller et al. 2006) suggest that availability of alternative foods for predators can depress rates of nest predation. In our system, most species of nest predators are omnivorous, opportunistic generalists (e.g., raccoon, American Crow) that are known to regularly consume anthropogenic foods in metropolitan areas. Moreover, because these species

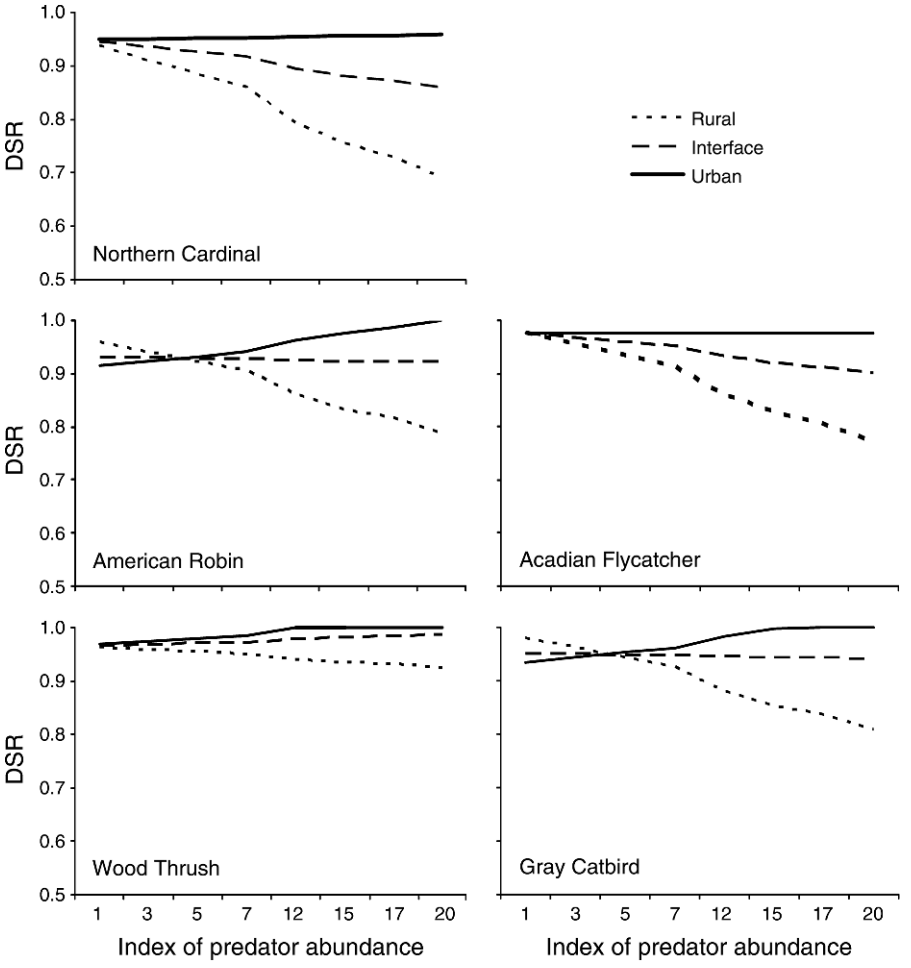

FIG. 2. The relationship between daily survival rate (DSR) and an index of predator abundance changes among urban (urban index = 1.5), urban–rural interface (urban index = 0), and rural (urban index = −1.2) landscapes.

readily move between the urban matrix and forests (Oehler and Litvaitis 1996, Barratt 1997, Pedlar et al. 1997, Prange et al. 2004), they can access a wide range of anthropogenic foods. Our previous research demonstrates that urban landscapes supply greater numbers of birdfeeders, abundant fruiting exotic plants, and residential and commercial buildings with trash receptacles (Borgmann and Rodewald 2005, Atchison and Rodewald 2006, Leston and Rodewald 2006).

Our finding that nest predator activity increased as landscapes became more urbanized is consistent with other studies. Metropolitan areas are widely known to support greater densities and/or activity levels of many generalist and opportunistic predators (Crooks and Soulé 1999, Sorace 2002, Gehrt 2004, Prange and Gehrt 2004, Chace and Walsh 2006). Such positive responses of generalist predators to urbanization may stem from urban-associated changes in anthropogenic food resources as well as other ecological changes, such as the warmer winter temperatures and altered vegetation structure in urban forests in our system (Atchison and Rodewald 2006, Leston and Rodewald 2006; Rodewald, *in press*). An important caveat is that, like most others, we may have poorly sampled nocturnal predators and our index of predator abundance reflects activity levels more than true densities. That said, the patterns that we report here are consistent with our recent data (2007–2009) from distance-based surveys (i.e., density estimates are adjusted for detection probability) and scent stations deployed with camera traps (i.e., to better sample nocturnal mammals; A. Rodewald and L. Kearns, *unpublished data*). Activity, as measured by number of encounters or detections, is arguably the most appropriate metric to use for understanding the trophic role played by predators and the predation risk experienced by breeding birds. Nevertheless, more research is needed to understand the population responses of predators to anthropogenic food subsidies and how predator abundances may be related to foraging behavior.

As reported in other studies, we found correspondence between nest predation and predators, but this relationship was only evident in the rural landscapes. The apparent link between rates of nest predation and avian nest predators, especially corvids, is well established (Andrén 1992, Zanette and Jenkins 2000, De Santo and Willson 2001, Luginbuhl et al. 2001, Roos 2002, Marzluff et al. 2007). Positive associations between nest predation and numbers or activity levels of predators also are reported for rodents (Schmidt and Ostfeld 2003*a*, *b*, Cain et al. 2006), mustelids (Cain et al. 2006), and snakes (Zanette and Jenkins 2000).

Others have reported apparent mismatches between super-abundant predators in urban areas and the degree to which those species are responsible for depredation events, though few have been explicitly tested. Despite rising in number in many European cities, Black-billed Magpies (*Pica pica*) minimally impacted songbird productivity, even for species known to be sensitive to predation by corvids (Chiron and Julliard 2007). Likewise, the abundant predatory Hooded Crow (*Corvus cornix*) accounted for $<1\%$ of nest depredations on shrub-nesting songbirds in Czech Republic cities (Weidinger 2009). In our study we also found that relative abundance of urban predators was not associated with reduced nesting success of forest songbirds. However, we were unable to either document the actual reliance of predators on anthropogenic resources or experimentally test if anthropogenic resources prompted the patterns we report.

Other possible explanations for the disconnect between nest survival and predator activity include predator swamping (Darling 1938) and shifts in habitat or behavior that reduce vulnerability to nest predation in urban areas. Although high numbers of cardinals and robins at urban sites might suggest predator swamping, spot-mapping data from 2004–2009 indicate that overall territory densities of understory and midstory-nesting birds were similar, with an annual average of 13.0 territories per 2 ha in rural and 13.3 in urban forests (A. Rodewald, *unpublished data*). The ability of predators to detect or depredate nests might be reduced if urban birds had access to higher quality or safer nest sites, made fewer provisioning trips, and/or increased nest attendance rates, which might be expected if birds used readily available anthropogenic foods. However, previous research indicates that (1) urban cardinals made greater numbers of nest-provisioning trips to nests than rural birds (Leston 2005), (2) nest attendance by cardinals during incubation ($\sim$30 min/h) was similar among sites and unrelated to daily survival rates (Smith-Castro and Rodewald 2010*a*, *b*), and (3) the most common nest substrate in urban forests (i.e., the exotic shrub, Amur honeysuckle [*Lonicera maackii*]) was associated with increased risk of nest predation compared to other substrates (Borgmann and Rodewald 2004, Rodewald et al. 2010).

The ways in which predators and prey interact are likely to change as the human footprint continues to expand. In North America alone, 60% of mesopredator species have shown range expansions, likely due to the combined effect of removal of apex predators (i.e., mesopredator release), land use changes, and human-associated food resources (Prugh et al. 2009). Regional populations of generalist and opportunistic mesopredators are likely to continue to swell as landscapes continue to urbanize. Our work shows that there is potential for predator–prey relationships to become decoupled when synanthropic predators are subsidized by anthropogenic resources. In this way, human drivers can alter species interactions that are well established in less-developed systems. Our findings underscore the importance of understanding socioecological processes that operate within cities.

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